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VOLUME XLV NUMBER 6

BOTANICAL GAZETTE

JUNE 1908

RELATION OF MEGASPORES TO EMBRYO SACS IN ANGIOSPERMS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY **110**

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The recorded cases of unusual conditions in the angiosperm embryo sac are multiplying. Especially is this true in reference to the occurrence of more than eight nuclei in the ante-fertilization development of the gametophyte. There is a tendency to regard the latter cases as representing a more primitive condition of the gametophyte, and to exclude from consideration a general view of the genesis of the nuclei. It seems to be a fitting time to call attention to certain facts that may interpret this situation, may connect it with other "irregularities," may check the tendency to ill-considered generalization, and may indicate certain things that must be included in any investigation of the embryo sac.

In the genesis of the ordinary angiosperm embryo sac from the megaspore mother cell five successive nuclear divisions are involved, the first two being the reduction divisions (usually resulting in four megaspores with walls), and the other three resulting in the production of eight nuclei from the nucleus of one of the megaspores. The functions of these eight nuclei of the female gametophyte do not enter into the present discussion. Attention is called to the following facts: this genesis begins with the division of the mother cell; the essential part of the process is found in the first two divisions, which cannot be omitted, so far as we know, when fertilization is to occur; the result of these first two divisions is the organization of megaspore nuclei, definitely recognized by their cytological history and structure.

The most familiar illustration of departure from this ordinary sequence is the case of Lilium and its allies. In current description the mother cell of Lilium is said to "function directly as a megaspore," and the resulting eight-nucleate sac seems to be quite normal. The inference is that the formation of megaspores has been omitted, and that the nucleus of the mother cell holds the same relation to the eight nuclei of the embryo sac that the megaspore nucleus does in ordinary cases. Analysis of the situation, however, shows that this is not true, for megaspores, at least their nuclei, cannot be omitted. The first two divisions from the mother cell are reduction divisions, and therefore the first four nuclei of the embryo sac of Lilium are megaspore nuclei, to be recognized as such by their cytological history and structure. This means that the nuclei of four megaspores have entered into the structure of the female gametophyte of Lilium; and that to complete its ante-fertilization development each of these nuclei divides once. Therefore, in the case of Lilium, there is only one division after the reduction divisions, instead of the usual three; and the total number of divisions is reduced from the customary five to three. In this case the history of an embryo sac containing the usual structures shows a very unusual reduction in the number of successive divisions, and this reduction seems to have been attained by many more monocotyledons than dicotyledons.

The case of Cypripedium[1] is an illustration of a similar reduction; but with the old methods of interpretation it would stand as remarkably different from Lilium and most angiosperms, for the completed embryo sac, ready for fertilization, contains only four nuclei. But in this case the mother cell divides, and one of the daughter cells forms the embryo sac. The first division of the nucleus of this daughter cell is the second reduction division, resulting in two megaspore nuclei. It is these two megaspore nuclei that are involved in the development of the female gametophyte, each dividing once as in the case of Lilium. Therefore, in Cypripedium also the usual five successive divisions are reduced to three; the only difference being that in Lilium four megaspore nuclei are involved, while in Cypripedium only two are used. In her paper Miss PACE calls attention to this comparison, and also to the fact that the elimination of one more division would result in an oogenesis similar to that of animals.

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[1] PACE, LULU, Fertilization in Cypripedium. BOT. GAZETTE 44:353–374. *pls. 24–27.* 1907.

In the older papers many records of "three megaspores," "two megaspores," and "no megaspores" appear, which either must be due to incomplete investigation or represent such an elimination of divisions as is shown by Lilium and Cypripedium.

What has been regarded as the most striking exception to the usual structure of the angiosperm embryo sac is the case of *Peperomia pellucida*, described by CAMPBELL[2] and JOHNSON.[3] In this sac sixteen nuclei appear before fertilization; that is, there appears to be one more division than usual. Lately JOHNSON[4] has described a similar condition in the Jamaican *Peperomia hispidula*, in which there are also eight-nucleate sacs.

Fortunately, in the case of Peperomia we know that the mother cell does not divide to form walled megaspores, so that the probable interpretation of the situation is evident. Four megaspore nuclei are formed, all of which are probably involved in forming the female gametophyte. By two successive divisions each of these gives rise to four nuclei, and the result is sixteen nuclei. It follows that the ordinary number of successive divisions has been reduced from five to four; and that if Peperomia had suffered no reduction, there would have been thirty-two nuclei in the embryo sac. In number of divisions, therefore, Peperomia lies between the ordinary angiosperms on the one side, and Lilium and Cypripedium on the other. This condition should be regarded as advanced in the direction of the elimination of divisions, rather than primitive. If an embryo sac derived from a single megaspore should contain sixteen nuclei, it could be regarded as relatively primitive; but the sac of Peperomia could contain thirty-two nuclei and only be normal. *Peperomia hispidula* is interesting in developing eight-nucleate sacs in addition to the sixteen-nucleate ones, which perhaps puts it upon a level of reduction with Lilium. It may have some bearing on the situation to note also that JOHNSON in his account of this species described the first four nuclei of the sac as "arranged in a perfect tetrad," which would be quite natural for megaspores. In fact, it may not be out of place to state that JOHNSON has expressed the opinion privately that these four nuclei are those of megaspores.

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[2] CAMPBELL, DOUGLAS H., Die Entwicklung des Embryosackes von *Peperomia pellucida* Kunth. Ber. Deutsch. Bot. Gesells. **17**:452–456. *pl. 31.* 1899.

[3] JOHNSON, D. S., On the endosperm and embryo of *Peperomia pellucida.* BOT. GAZETTE **30**:1–11. *pls. 28, 29.* 1900.

[4] JOHNSON, D. S., A new type of embryo sac in Peperomia. Preliminary notice. Johns Hopkins Univ. Circ. **1907**:19–21. *pls. 5, 6.*

Recently CAMPBELL[5] has examined *Pandanus odoratissimus* and *P. Artocarpus*, and found usually fourteen nuclei in the embryo sac. At the four-nucleate stage there is the usual arrangement of two micropylar and two antipodal nuclei; but the former do not divide, and the latter give rise to twelve nuclei. If this record is confirmed by tracing the history of the nuclei, there is introduced in this case an irregularity in the succession of divisions. It may be assumed, subject to subsequent observation, that four megaspore nuclei are involved in the formation of these fourteen nuclei; and the irregularity would consist in the fact that two of them do not divide; that one of the others added two successive divisions (the elimination of one division); and that the remaining one added three successive divisions (the usual number). There is thus no greater number of divisions than usual, and even a certain amount of elimination. It is interesting to note that if the two micropylar nuclei do not divide and are really megaspore nuclei, the egg is removed from the mother cell by only two divisions, which is the condition of the animal egg. A careful cytological investigation of these divisions would seem to be most desirable.

The introduction of a certain amount of irregularity in the succession of divisions is suggested by the records of several species. For example, in Gunnera,[6] while eight nuclei are common, any number up to sixteen may be found; and in *Trillium grandiflorum*[7] ten sometimes occur. In neither of these species, however, do we have any information as to the behavior of the mother cell in forming megaspores.

In *Ulmus americana*[8] we know that the "mother cell functions directly as the megaspore," as in Peperomia, and in the majority of embryo sacs there are eight nuclei (the normal number of nuclei, but an elimination of two divisions); but sometimes there are "twelve or more nuclei" (meaning another division, but still one less than the usual number).

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[5] CAMPBELL, DOUGLAS H., The embryo sac of Pandanus. Preliminary note. Annals of Botany **22**:330. 1908.

[6] SCHNEGG, H., Beiträge zur Kenntniss der Gattung Gunnera. Flora **90**:161–208. *figs. 28.* 1902.

[7] ERNST, A., Chromosomereduction, Entwicklung des Embryosackes, und Befruchtung bei *Paris quadrifolia* L. und *Trillium grandiflorum* Salisb. Flora **91**: 1–46. *pls. 1–6.* 1902.

[8] SHATTUCK, CHARLES H., A morphological study of *Ulmus americana*. BOT. GAZETTE **40**:209–223. *pls. 7–9.* 1905.

The situation among the Araceae deserves attention, for great irregularities in the embryo sac have been observed.[9] In Aglaonema the nuclei are four to twelve; while in Nephthytis they are reported as ranging in number from two to twelve or thirteen. Unfortunately, in these cases we are not sure of the behavior of the mother cell; but so far as the records for Araceae go, the mother cell divides once or not at all. It is needless to draw any conclusions as to the amount of reduction involved in the four nuclei of Aglaonema or the two nuclei of Nephthytis until we know something of their history. At all events, there is a reduction of the ordinary number of divisions in these forms; and this is probably true even in the cases where twelve or thirteen nuclei appear.

The only case reported, in which there remains some evidence that an additional free nuclear division may occur, is that of the Penaeaceae, a small African group of shrubby xerophytes restricted to southwestern Cape Colony. In a preliminary note, STEPHENS[10] has announced his results with five species, representing three genera (Sarcocolla, Penaea, and Brachysiphon), and his account applies to all of them. There are sixteen free nuclei formed in the sac before fertilization, which are said to be derived from the innermost one of a row of three megaspores. In such a case three "megaspores" are as good as four, except that the outermost cell is not a megaspore. The testimony breaks down, however, at the critical stage, for the investigator is not certain as to the "row of three." Of course if it should turn out to be a "row of two," the megaspore condition would be that of Cypripedium, followed by the usual number of divisions. The behavior of the nuclei, however, suggests strongly that four megaspore nuclei are concerned, and that there is no "row" developed by the mother cell at all. It is a very interesting performance as described; for the original nucleus of the sac produces four nuclei in tetrahedral arrangement; these four separate and become parietally placed (one micropylar, one antipodal, two equatorial); each of the four produces a group of four nuclei; three nuclei of each group organize after the fashion of an egg apparatus; and the four free nuclei pass to the center of the sac and fuse to form the primary endosperm nucleus. We have here at least the assurance of simultaneous successive divisions, which we do not have in the case of all 16-nucleate sacs. If four megaspore nuclei are involved in this organization, the reduction in the number of successive divisions is just that which probably occurs in Peperomia.

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[9] CAMPBELL, DOUGLAS H., Studies on the Araceae. The embryo sac and embryo of Aglaonema and Spathicarpa. Annals of Botany **17**:665–687. *pls. 30–32.* 1903.

———Studies in the Araceae. III. Annals of Botany **19**:329–349. *pls. 14–17.* 1905.

[10] STEPHENS, E. L., A preliminary note on the embryo sac of certain Penaeaceae. Annals of Botany **22**:329, 330. 1908.

Some evident conclusions may be drawn from the above statement, and they should be of use in investigations of the angiosperm embryo sac. The nuclear divisions within the embryo sac vary in character; they may include both reduction divisions, the second one, or neither of them (the usual case). The appearance of more than eight nuclei in an embryo sac is no evidence that there has been any more than the usual number of successive divisions. As many as thirty-two nuclei may appear in an embryo sac without increasing the usual number of divisions. It is absolutely necessary to trace the nuclear succession from mother cell to completed embryo sac before any safe conclusions can be drawn as to the significance of the conditions observed within the sac. The cases of an increased number of nuclei, as in Peperomia, which have sometimes been cited as showing a primitive condition of the sac, have actually turned out to be cases of reduction from the ordinary condition. There is a tendency among many groups to eliminate the divisions that follow the two reduction divisions, but the tendency is not general among angiosperms, since among the Sympetalae it does not seem to exist; hence the forms which exhibit it may be regarded as more or less specialized in this feature.

If an angiosperm embryo sac should be found containing sixteen or more nuclei derived from a single megaspore nucleus, it may be regarded as relatively primitive; but such a sac has not yet been demonstrated.

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